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DEMOGRAPHY AND POPULATION BIOLOGY OF A RARE TARPLANT, *BLEPHARIZONIA PLUMOSA,* (ASTERACEAE) A CALIFORNIA SUMMER ANNUAL FORB

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Abstract

Blepharizonia plumosa (Kellogg) E. Greene, also known as the big tarplant, is a rare, summer-flowering, annual tarplant found in California grasslands. Although rare throughout its range, *B. plumosa* is numerous at the Lawrence Livermore National Laboratory (LLNL) experimental test facility, Site 300. We conducted a common garden experiment, a reciprocal transplant study, and a laboratory germination study to compare *B. plumosa* to its more common relative, *B. laxa* Greene (which is rare at Site 300), and to gather data on the basic biology of *B. plumosa* in preparation for a possible mitigation project. Three populations of *B. plumosa* were compared to a single population of *B. laxa.* Little population differentiation was found in *B. plumosa* in terms of transplant success. *Blepharizonia plumosa* expresses much more extreme dimorphism with respect to seed germination: ray seeds have low germination percentages (<4%) compared to disc seeds (50–78%, $P < 0.017$). *Blepharizonia laxa* did not show any significant differences between ray (18%) and disc (17%) seed germination ($P > 0.05$). *Blepharizonia plumosa* produced three times more ray seeds than disc seeds (ratio: 3.2), while *B. laxa* produced little over half as many ray seeds as disc seeds (ratio: 0.65). *Blepharizonia plumosa* plants grown from ray seeds have a lower biomass accumulation (<5 g per plant compared to 28 g per plant for *B. laxa,* $P < 0.017$) and none survived to flower production. Among ray-derived *B. laxa* plants, 70% survived to flower production. This difference in ray seed production and performance points to a possible basis for ecological differences between the two species. Until the mechanisms controlling dormancy are more clearly understood, only disc seeds should be used in the creation of new populations of *B. plumosa.*

Annual plants within California grassland communities are often divided into functional groups based on their flowering period, e.g., early grasses, late grasses, early forbs, and summer forbs (Pendleton et al. 1983). Due to the changes in climate throughout the growing season, plants within these groups are confronted with a wide range of environmental conditions, e.g., changing soil moisture content and photoperiod. Compared to the early spring flora, relatively little ecological information appears to be available on the annual summer forbs. These summer forbs, or late forbs, include species of the tarplant subtribe *Madiinae* (Compositae), e.g., *Hemizonia, Madia,* and *Calycadenia,* as well as *Blepharizonia.* Information on species in the summer flora is important for conservation and habitat restoration activities. For example, 110 late-flowering (July–September) taxa listed by the California Native Plant Society (CNPS) are of conservation concern. Of these, eight taxa are state or federally listed as threatened or endangered (Skinner and Pavlik 1994).

The flowering period of summer forbs, such as *Hemizonia* (Chiariello 1989) and *Blepharizonia* (personal observation), starts in late July or early August and can extend into November. Because of their late-flowering period, summer forbs spend much of their lifetime in the harsh California summer drought. They are able to survive drought conditions by developing deep root systems and are able to escape the higher temperatures that occur at the soil surface due to their height (Morse 1988). In water usage studies conducted by Gulman et al. (1983), it was found that a spring-flowering plant (*Clarkia*) and a summer-flowering plant (*Hemizonia*) differ in their access to stored water in the post-precipitation season. *Hemizonia* has the ability to root into deeper non-nutritive substrate for water, while *Clarkia* cannot. In addition to being able to access additional water, summer flowering plants postpone water stress through hydrophilic, pectinaceous, extracellular polysaccharides concentrated in leaf tissue (Morse 1988) and are able to flower at lower water potentials (Chiariello 1989). Schoenherr (1992) points out that by postponing the flowering stage into the summer months, summer forbs have less competition for pollinators.

Later-blooming plants accumulate an order of magnitude more biomass than earlier-blooming plants (Mooney et al. 1986) and may also have some additional colonization advantages. First, naturally disturbed sites, such as gopher mounds, can be ideal for colonization. The later a species flowers, the larger the number of mounds available. Second, since late-flowering species tend to be taller than spring-flowering species, their seeds

have a wider dispersal radius. This allows them to colonize mounds and other disturbed areas farther from their immediate neighborhood (Hobbs and Mooney 1985).

Blepharizonia plumosa (Kellogg) E. Greene is an extremely rare late-flowering plant included on the CNPS List 1B (Skinner and Pavlik 1994, under the former moniker *Blepharizonia plumosa* subsp. *plumosa*[1]), which includes plants that are rare, threatened, or endangered. The CNPS R-E-D code (rarity-endangerment-distribution) for *B. plumosa* is 3-3-3, which indicates that this plant is limited to one or several restricted populations, is endangered throughout its range, and is endemic to California. The CNPS also noted that possibly the only remaining populations exist on private property in the hills near Livermore, California. Populations have been previously identified in Alameda, Contra Costa, San Joaquin, Stanislaus, and Solano Counties (Skinner and Pavlik 1994). Preston (1996) noted that a population was discovered at Contra Loma Regional Park, south of Antioch in 1979, but that surveys conducted by the East Bay Regional Park District in 1991 were unable to relocate the species. In 1994, several more populations were discovered on private property southwest of Brentwood (CNDDB 1996). Another small population was found at Chaparral Springs near Mount Diablo (Preston 1996). Current status of these populations is unknown.

Several populations of *B. plumosa* were identified during a habitat survey in 1996 at Lawrence Livermore National Laboratory's (LLNL) experimental test facility (Site 300). A few populations of the more common big tarplant, *Blepharizonia laxa* Greene, were also found. *Blepharizonia laxa,* although also endemic to California, exists in plentiful numbers and has a much larger range which extends farther south into the inner South Coast Ranges, including San Benito County (Hickman 1993). Site 300 is a high-explosive test site operated by the University of California for the Department of Energy. The site is closed to the public and has had no agricultural activity since its establishment in the 1950s. The botanical diversity of the site may be due to its lack of public access, lack of agricultural activity, and high burn frequency. Large stands of the native perennial bunchgrass, *Poa secunda* J.S. Presl, occur in the northern portion of the site and are thought to be maintained by the annual late spring/early summer controlled burns conducted for wildfire control (Carlsen et al. 2000). The large-flowered fiddleneck, *Amsinckia grandiflora* A. Gray (Boraginaceae), which is on the state and federal endangered species lists (Schoenherr 1992), and the diamond-petaled poppy (*Eschscholzia rhombipetala* E. Greene), which was until recently thought to be extinct (Hickman 1993), are both found at Site 300. While historical occurrences of many rare plants probably have been extirpated by agricultural activities and nonnative plant colonization (Skinner and Pavlik 1994), these factors may be reduced at Site 300.

While the rarer taxon, *B. plumosa,* is quite common at Site 300, occurring most plentifully in areas that are routinely burned, *B. laxa* is uncommon at Site 300, but exists in both unburned and burned areas. The two species are known to co-occur at only two locations, one of which is routinely burned. That the two species appear to differ in their habitat requirements may indicate some ecological differences between them. Comparison of rare and common congeners can provide important information for rare plant management (Pantone et al. 1995) and can illuminate differences that affect comparative abundance (Byers 1998).

For conservation and management purposes, a thorough understanding of the population dynamics and the feasibility of population restoration of *B. plumosa* are critical. Mitigation of a *B. plumosa* population may need to be performed at Site 300 in the future, but few reintroduced populations of endangered species appear to be self-sustaining (Pavlik 1994; Parsons and Zedler 1997; Pavlik and Espeland 1998). Allen (1994) stated that only four of the 45 reintroduction projects undertaken in California during the past decade were successful when judged by survival and reproduction. In many instances, reintroduction failure was attributed to poor planning or lack of information about the species (Hall 1986; Pavlik 1994). Population restoration is often performed without regard to the level of microhabitat adaptation in source populations (Knapp and Rice 1994). Small-scale adaptation in source populations can prevent success in restoration attempts (Dyer and Rice 1997). However, in situ population differentiation is not necessarily negatively correlated to transplant success (Meagher et al. 1978); thus each of the three *B. plumosa* populations were compared for transplantability in our experiment.

We initiated a study in November of 1996 to collect basic demographic and population biology data on *B. plumosa.* The study was needed to determine if population differentiation in *B. plumosa* occurs with respect to transplant success and also to examine differences between *B. plumosa* and the more common big tarplant, *B. laxa.* The study included a common garden experiment followed by a field reciprocal transplant study to investigate field germination rates. In addition, a laboratory germination study was conducted to investigate the relationship between seed type, seed age, and germination/dormancy. Because so little is known about population biology of *B. plumosa,* and because ongoing activities at Site 300 could poten-

[1] The *Blepharizonia* genus has recently been revised (Baldwin et al. 2001): *Blepharizonia plumosa* was formerly *B. plumosa* subsp. *plumosa* (Hickman 1993), while *Blepharizonia laxa* was formerly *B. plumosa* subsp. *viscida* (Hickman 1993).

tially impact the populations there, these data could be used both to improve management practices and to prepare for a possible onsite mitigation project at Site 300.

Materials and Methods

Study species. Both *B. plumosa* and *B. laxa* are dicots within the family Asteraceae, and members of the tribe Helenieae (Karis and Ryding 1994). They are both summer annual forbs, which germinate with the onset of the first substantial fall/winter rains and flower July–October. One of the common attributes to this family is heterocarpy, or the production of two or more single-seeded fruit types (achenes) on a single plant. Although the term "seed" should be used when addressing germination and dormancy, and fruit or achene should be used when addressing morphology, the term "seed" will be used solely throughout this paper. In the case of *Blepharizonia,* the plants have dimorphic flowers within the same inflorescence. Seed dimorphism is very common in the plant kingdom, found in the families such as Asteraceae, Chenopodiaceae, Poaceae, Brassicaceae, and is often associated with arid or disturbed environments (Harper 1977; van der Pijl 1972). As discussed by Bremer (1994), seed morphology is among the most important and useful features in Asteraceae classification at the generic and species levels.

The two species can be distinguished from one another by seed morphology and leaf color (Hickman 1993; Baldwin et al. 2001). The most distinctive characteristic of *B. plumosa* is the pappus on the disc seed that is 1.5–3 mm in length. The disc seed pappus is sometimes described as plumose (thus the specific epithet *plumosa*) and contrasts with the very minute pappus of the ray seeds (Fig. 1). The plants also have a pale green color, as their foliage is sparsely glandular below the inflorescence. Older plants have many inflorescences on side branches.

The disc and ray seeds of *B. laxa* appear much more similar to the naked eye and have a short pappus from 0–1 mm in length. *Blepharizonia laxa* is much more glandular than *B. plumosa* giving the plant a more yellow-green color and a much stronger scent. *Blepharizonia laxa* also tend to be slightly taller than *B. plumosa* (personal observation). Older plants have inflorescences mostly terminal on slender wand-like, bracted peduncles (Hickman 1993).

Study site. Corral Hollow is a valley of the Inner Coast Ranges that contains examples of native plants and animals characteristic of the Great Central Valley. This area has been used primarily for grazing sheep and cattle (Schoenherr 1992). Site 300 covers 2711 ha and is located in the Altamont Hills of the Diablo Range separating the Livermore and San Joaquin Valleys. The southern portion of Site 300 (T3S R4E sect. 29 SW ¼) extends into Corral Hollow and consists of rugged north/south-trending canyons of elevations ranging from 150 m to over 500 m. It is primarily a grassland-dominated site, with sparse populations of coastal sage scrub and blue oak woodland in the southwest corner of the site.

Three populations of *B. plumosa,* designated B834 Berm, B834 Drainage, and B850, and one population of *B. laxa,* designated Middle Canyon, were used in this study. Figure 2 shows Site 300 and the locations of the study populations. Table 1 includes some habitat characteristics of all four populations.

Common Garden Experiment

Intact inflorescences containing seeds were collected in October and November 1996 from the three populations of *B. plumosa* and the single population of *B. laxa.* Following collection, they were segregated into disc and ray seeds. A large container of soil (approximately 60 liters) was also collected in November 1996 from each of the four population sites. No attempt was made to insure the soil was free from existing seeds. A fifth container was filled with potting soil. Each container was divided into four quadrants, each of which was then divided in half. Each quadrant was assigned a source population and its two sub-quadrats delineated disc and ray seeds. In late November 1996, 25 disc and 25 ray seeds from each population were planted into adjacent sub-quadrants in each container, as shown in Fig. 3. Germination was allowed to occur naturally following rainfall events, although all containers were later outfitted with a drip irrigation system to ensure even watering. Germination and growth were closely monitored for approximately 10.5 months, until October 1997. Other species that germinated within the pots were removed. Any *B. plumosa* or *B. laxa* plants that emerged in locations not associated with the planting arrangement were also removed. Seeds were collected from plants as they matured and biomass was collected after senescence.

Data analysis. Percent germination for disc and ray seeds was calculated by population in each of the soil types. To determine if differential germination was occurring, the average percent germination for all seeds planted in native soil ($n = 4$) was compared to that of all seeds planted in non-native soil ($n = 12$). Because no significant relationship was found between soil type (native vs. non-native) and the amount of germination ($P > 0.95$) or percent survivorship ($P > 0.19$), each pot was treated as a replicate for all further data analyses. Percent germination for seed type was calculated by dividing the final number of germinated seeds by the total number planted ($n = 25$). Then, the average percent germination was calculated by taking the mean across all replicates ($n = 5$). The percentage of plants surviving to flower production

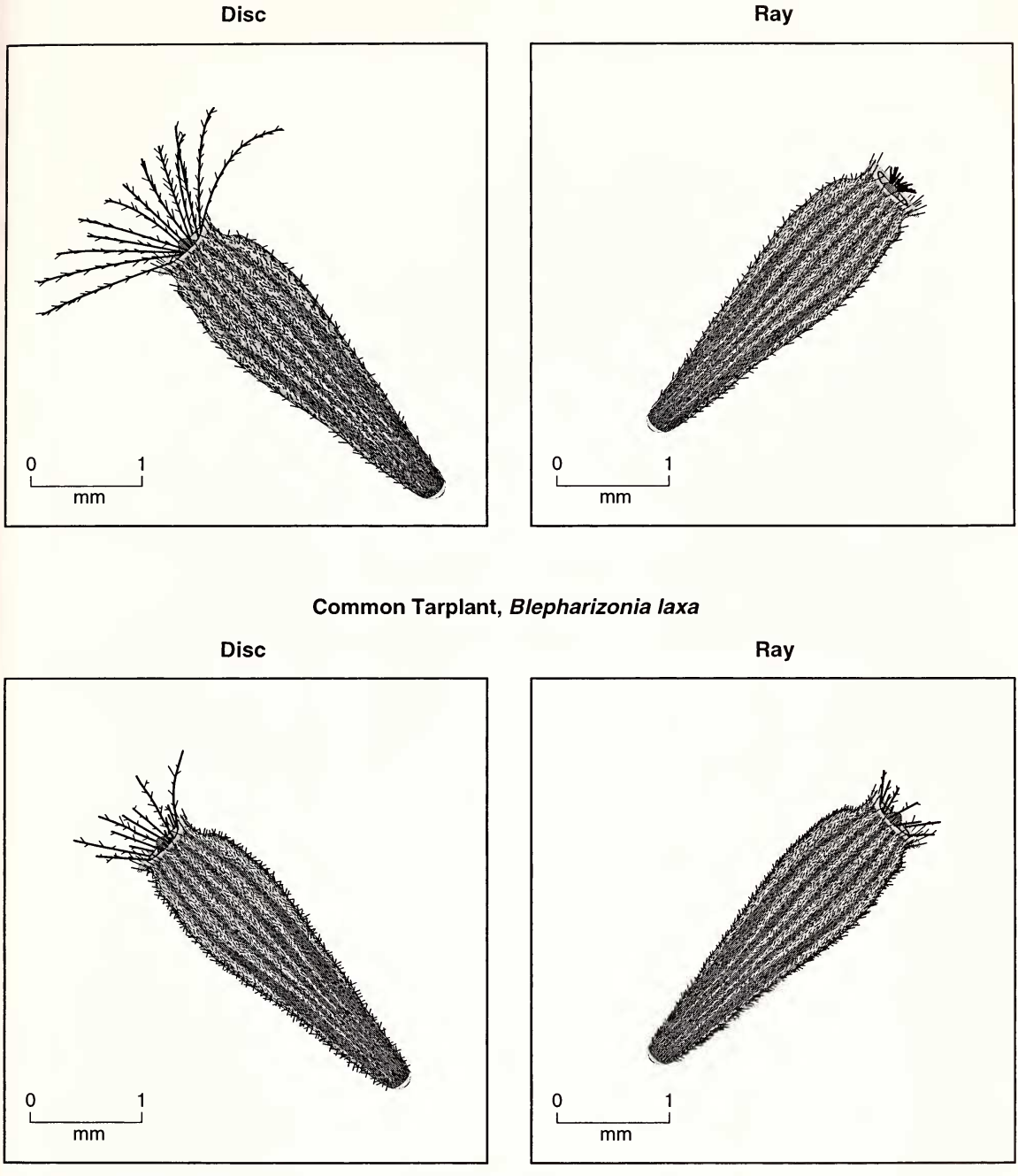

FIG. 1. Comparison of pappus on seeds of *Blepharizonia plumosa* and *B. laxa*.

was calculated by dividing the number of flower-producing plants by the number of plants that germinated, then averaging across replicates (n = 5). Average seed production per plant is the total seed production per replicate divided by the number of plants of the parent seed type in that replicate that produced mature seeds. All five replicates were then averaged. Statistical analysis of seed production was performed on the ratio of ray to disc seeds that each plant produced. Average biomass was calculated by summing the dry weights (in grams) of the plants collected in each replicate divided by the number of plants, then taking the mean across all replicates (n = 5).

Statistical analyses were performed using the general linear model in SAS, version 6 (SAS 1990). All percentage data were arcsine transformed prior to analyses. Single degree of free-

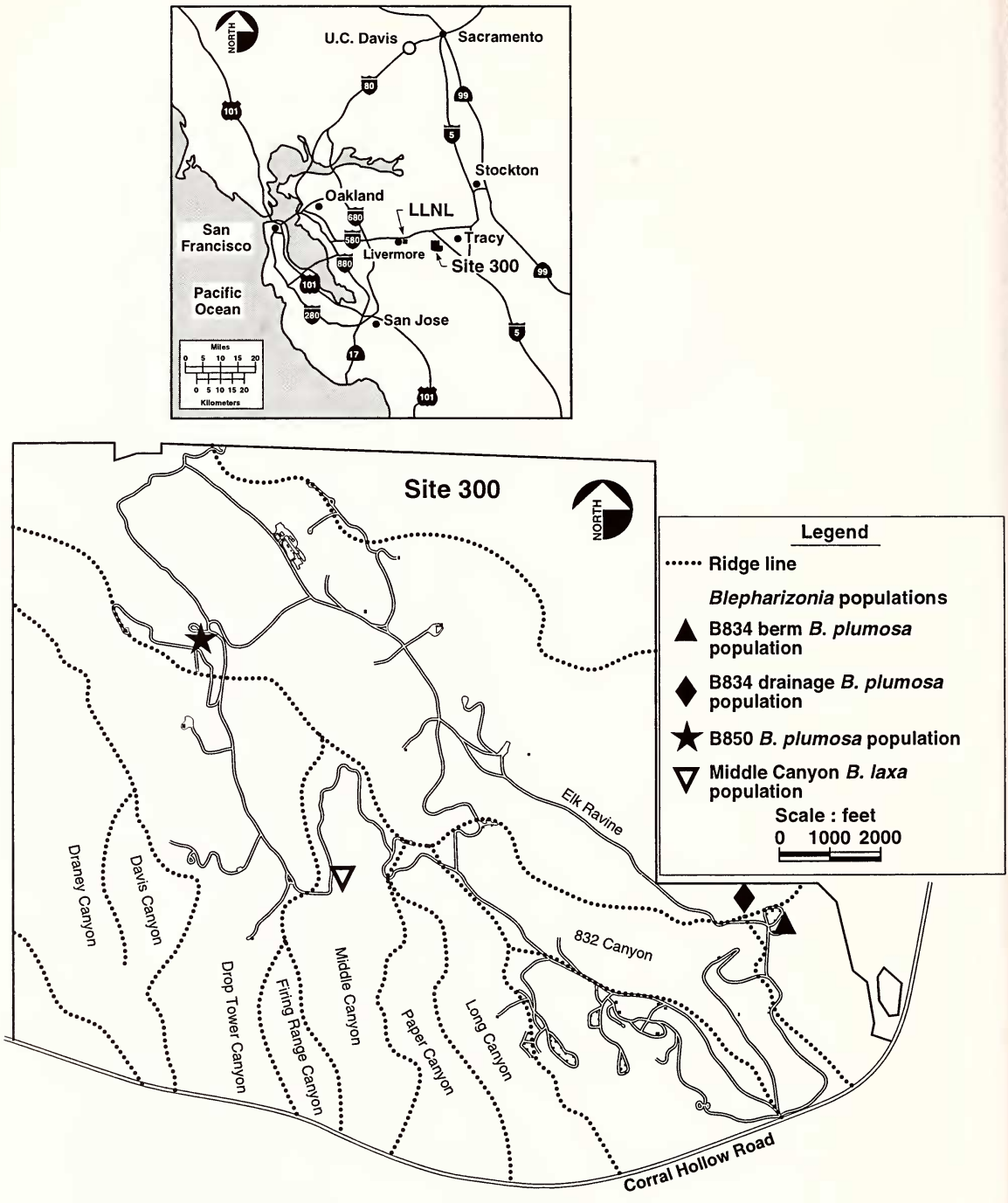

FIG. 2. Site 300 and locations of *Blepharizonia plumosa* populations.

dom f-tests (orthogonal contrasts) were performed to ascertain if differences occurred between disc and ray seeds within each species and then if differences occurred between the two species within each seed type. Tukey's separation of means was performed to determine if populations of *B. plumosa* were different from each other. Because of the multiple tests performed on the same data sets, a corrected alpha value was used to determine significance. Using a Bonnferroni correction, we divided our starting alpha value of 0.05 by three (the number of comparisons performed upon each dataset), so a test would have to have a P value of less than 0.017 to be signif-

TABLE 1. HABITAT CHARACTERISTICS OF THREE *BLEPHARIZONIA PLUMOSA* POPULATIONS AND ONE *B. LAXA* POPULATION AT SITE 300 (ADAPTED FROM PRESTON 1996).

Population	Number of plants	Plant community	Elevation (m)	Aspect	Slope (%)	Soil type	Management practices
B834 Berm (*B. plumosa*)	≈200	exotic annual grassland, *Avena* sp., *Gutierrezia californica, Eriogonum angulosum, Bromus diandrus, Holocarpha obconica*	≈315	north	8–30	clay, Alo-Vaquero complex	not burned, berm with low grass cover
B834 Drainage (*B. plumosa*)	500–1500	exotic annual grassland, *Bromus hordeaceus, B. diandrus, Amsinckia intermedia, B. madritensis* ssp. *rubens, Grindelia camporum.*	≈215	north	50–75	sandy to clay loam, Wisflat-Arburua-San Timoteo complex	annually burned
B850 (*B. plumosa*)	≈100	disturbed annual grassland, *Avena* sp., *Bromus madritensis* ssp. *rubens, Vulpia myuros*	≈400	north	30–50	rocky sand to clay loam, Wisflat-Arburua-San Timoteo complex	annual burned
Middle Canyon (*B. laxa*)	not determined	exotic annual grassland, *Avena* spp., *Bromus diandrus, B. rubens, B. hordeaceus, Hordeum marinum, Silybum marianum, Marah fabaceus, Gutierrezia californica, Phacelia distans*	≈400	east	50–75	sandy to clay loam, Wisflat-Arburua-San Timoteo complex	not burned

icant. This correction decreases our chance of rejecting the null hypothesis erroneously.

Reciprocal Transplant Study

Four 100-m^2 plots were established within each of the three *B. plumosa* populations. Disc and ray seeds from the common garden experiment were used in this study. As shown in Fig. 4, seeds were planted five across in four rows, each row corresponding to one of the four populations. Each plot was subdivided; one subdivision was assigned to disc seeds and the other to ray seeds. The seeds were spaced 11–12 cm apart within each row, each row was spaced six to seven cm apart, and each subdivision was spaced 11–12 cm apart. Seeds were planted in all four plots in each of the three *B. plumosa* populations. At the time of planting, seed placement was marked using colored plastic straws 10 cm in length. Upon germination, the seedlings were marked by placing a circle of string loosely around the base of the plant. The germination rate, growth, and survival of all marked plants were monitored throughout the season.

Data analysis. There was no difference in germination between locations for any parent population ($P = 0.544$), so data from all locations were pooled for analysis. Percent germination was calculated for each plot by source population and seed type. The individual plot values were then averaged ($n = 4$). Finally, the mean for the three populations or transplant locations was found ($n = 3$). Statistical analyses were performed in the same manner as those for the common garden study.

Laboratory Germination Study

Inflorescences were collected from the three *B. plumosa* populations and the *B. laxa* population in 1996, 1997, and 1998, and from the common garden experiment pots in 1997. All were collected in autumn (September–November) at the predispersal stage. The material was sorted into disc and ray seeds and stored at room temperature. Only seeds that appeared to be undamaged and fully mature were selected for use in the germination study. The seeds selected from the 1996 and 1998 collections were taken from native populations. However, due to the limited number of suitable seeds collected from the native populations in 1997, seeds from the common garden experiment were used for this year. For the *B. plumosa* populations, three replicates of 20 ray seeds and three of 20 disc seeds were used. Six replicates of 20 ray seeds and six of 20 disc seeds were used for the *B. laxa* population. Germination was initiated on 30 Nov 1998 for seeds collected in 1996 and on 1 Dec 1998 for seeds collected in 1997 and 1998. Seeds were placed in plastic Petri plates on Whatman 80 filter paper moistened with deionized water. The plates were then sealed with parafilm to reduce water evaporation

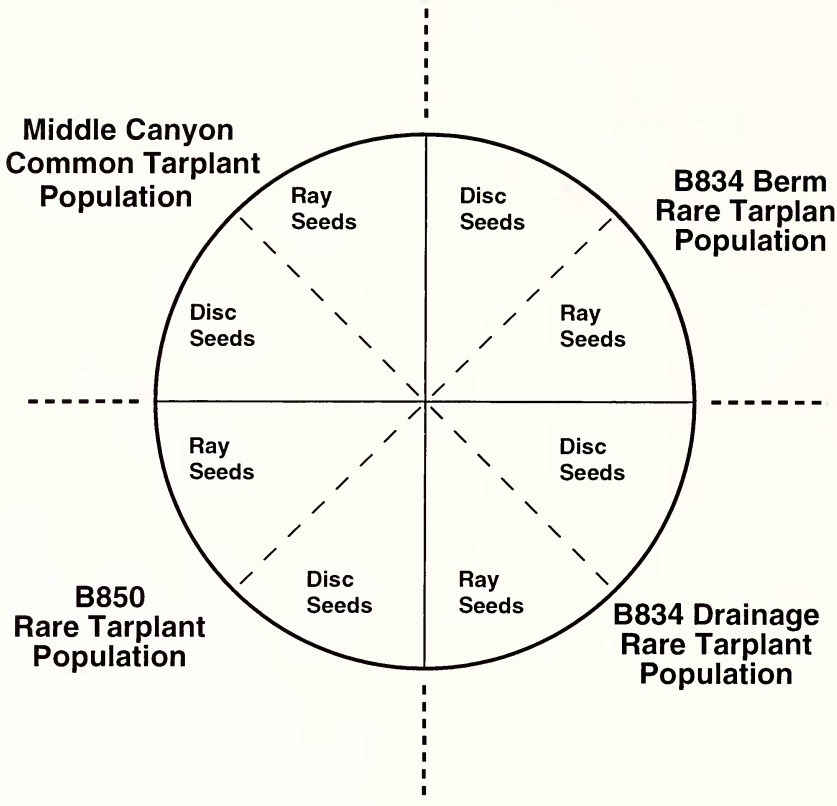

FIG. 3. Planting arrangement of tarplant seeds within each of five containers in the common garden experiment.

and placed in a dark cooler kept at room temperature. Germination data were collected for approximately six weeks (43 days) following initial wetting of the plates. All plates were wet again at the end of Week 1 (Day 8) and Week 2 (Day 16). At the end of Week 4 (Day 36), 60 percent of the plates were rewet as necessary. Germinules were removed as they germinated to control for any possible post-germination effects.

Data analysis. Percent germination was found by dividing the number of germinated seeds by the total number of seeds in the plate. Because some of the seeds selected were later determined to be immature, the number of seeds per plate ranged from 13 to 20. The seeds that did not germinate were examined under a dissecting microscope at the end of the experiment and designated as immature if they lacked an embryo. The individual plate values were then averaged by seed type, population, and year (n = 3 for *B. plumosa,* n = 6 for *B. laxa*). Cumulative germination represents final percent germination values. Final germination percentages were arcsine transformed and analyzed for age and subspecies effects using the general linear model in SAS, version 6 (SAS 1990). Fruit age (0, 1, or 2 years) was plotted against final percent germination for ray and disc seeds in *B. plumosa* and *B. laxa* using a least-squares linear regression (SAS 1990). Because three analyses were run on the same dataset (linear regression by species and by seed type plus a general linear model), our corrected alpha value was 0.05 divided by 3 to determine our significant P value (0.017).

RESULTS

Common Garden Experiment

Table 2 presents the results and statistical analyses of the germination rates, survivorship, and biomass production for the common garden experiment. A dramatic difference was observed in percent germination between the disc seeds and ray seeds for *B. plumosa.* Germination of the *B. plumosa* disc seeds ranged from 50 to 78%, while ray seed germination was below 4%. No statistical difference was observed between disc and ray germination for *B. laxa.* Although *B. plumosa* disc seeds appeared to have a higher level of germination than those of *B. laxa* disc seeds, and the inverse was true for ray seeds, due to the small sample size and high amount of variability within the *B. laxa,* these differences were not significant. A priori comparisons showed that there were no differences between *B. plumosa* populations for ray and disc germination.

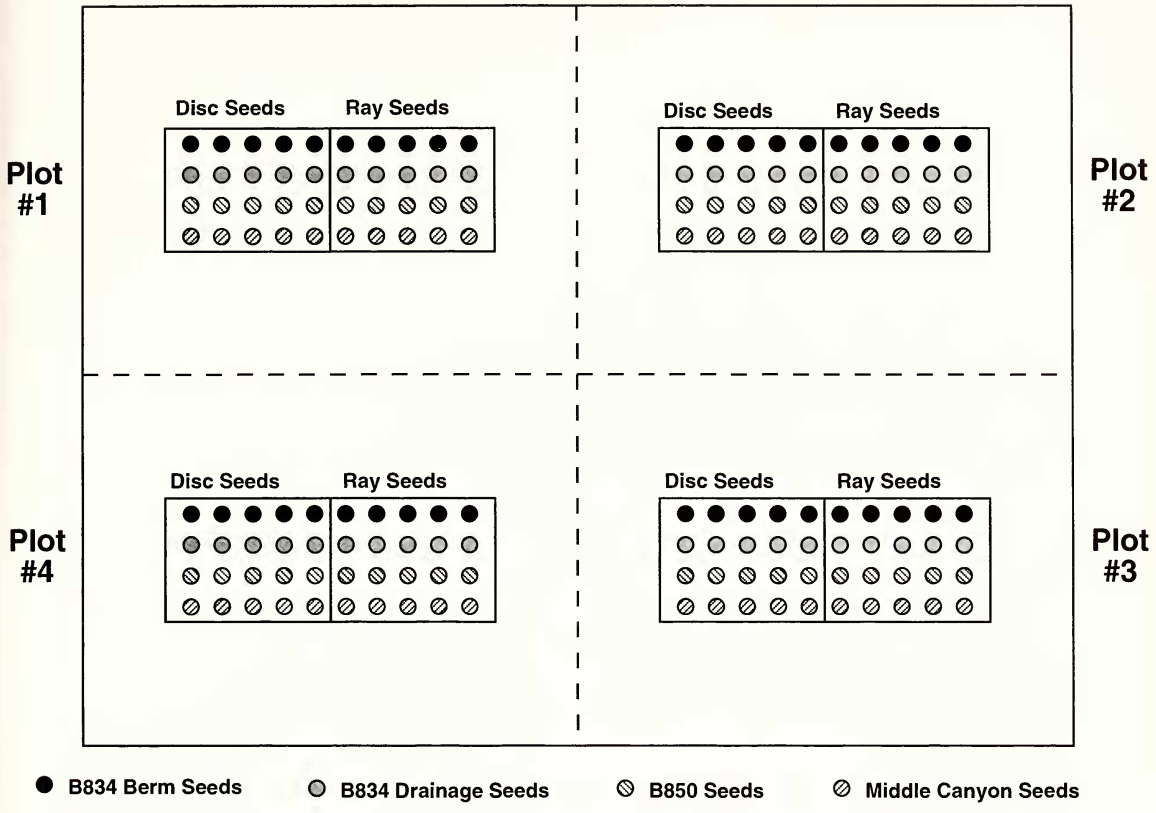

FIG. 4. Diagram of reciprocal transplant study within each of three tarplant field populations.

When comparing the percentage of tarplants surviving to flower production in the common garden experiment, a survivorship difference was apparent between the disc- and ray-seed derived plants for the *B. plumosa*. No ray-derived *B. plumosa* plants survived to flowering. However, because of the large difference in sample size (n = 7 ray-seed derived plants compared to n = 231 disc-derived plants) statistically significant differences were not found. No significant difference in survivorship was found between disc- and ray-derived *B. laxa* plants. Also, no difference in survivorship was found between *B. plumosa* and *B. laxa* disc-derived plants. However, a significantly lower percentage of *B. plumosa* ray-derived plants survived to flower production when compared to *B. laxa* ray-derived plants. As already mentioned, none of the *B. plumosa* plants from ray seeds survived, while 70% of *B. laxa* plants from ray seeds survived to flower production (n = 9). A priori comparisons showed that there were no differences in survivorship between *B. plumosa* populations.

When comparing biomass production, no difference per plant between disc- and ray-derived plants was found in either *B. laxa* or *B. plumosa*. The *B. laxa* plants, however, achieved much higher biomass (average 28 g) for ray-derived plants than *B. plumosa* ray-derived plants were able to accumulate (each plant less than 5 g).

The average seed production per plant is shown in Figure 5. Statistical analyses found an interaction between parent morph and seed morph ratio for *B. plumosa* and *B. laxa* ($P < 0.0005$). The ratio of ray to disc seed production from disc-derived *B. plumosa* plants was 3.2, while the ratio from the disc-derived *B. laxa* plants was 0.65, meaning that more similar numbers of disc and ray seeds were produced from the *B. laxa*. Again, no seeds were produced by the ray-derived *B. plumosa* (none survived to reproductive maturity). Ray-derived *B. laxa* produced many more disc seeds (average = 185) than ray seeds (average = 59). Several of the disc-derived *B. laxa* plants died prior to complete maturation of the seeds, which may account for the low numbers of seeds produced by these plants.

Reciprocal Transplant Study

The results and statistical analyses for germination rates in the reciprocal transplant study are presented in Table 2. As in the common garden experiment, a significantly higher amount of germination was observed for disc seeds than for ray seeds for *B. plumosa*, but no difference was observed between disc and ray germination for *B.*

TABLE 2. GERMINATION, SURVIVORSHIP, AND BIOMASS RESULTS OF THE RECIPROCAL TRANSPLANT AND COMMON GARDEN EXPERIMENTS (AVERAGE ± 1 SE). Differential shading between ray and disc categories indicates significant difference at $P < 0.017$ in the rare tarplant (*B. plumosa*). [a, b, ab] Different lowercase letters indicate significant differences among *B. plumosa* populations for disc seeds at $P < 0.017$. [A, B, AB] Different uppercase letters indicate significant differences among *B. plumosa* populations for ray seeds at $P < 0.017$. [*, **] Different symbol repetitions indicate significant differences between species for disc seeds at $P < 0.017$. [#, ##] Different symbol repetitions indicate significant differences between species for ray seeds at $P < 0.017$.

		Common garden			Reciprocal transplant
Parent population		% germination	% survivorship	Average biomass (g)	% germination
B834 Berm					
B. plumosa	Disc	77.6 + 5.46 [a*]	33.4 ± 14.0 [a*]	2.28 ± 0.54 [a*]	35.00 ± 11.55 [a*]
	Ray	1.6 ± 0.98 [A#]	0 ± 0 [A#]	0 ± 0 [A#]	3.3 ± 1.67 [A#]
Ratio (Ray:Disc)		0.021	0	0	0.094
B834 Drainage					
B. plumosa	Disc	49.6 + 0.98 [a*]	49.8 ± 15.2 [a*]	3.04 ± 0.73 [a*]	65.00 ± 2.89 [b*]
	Ray	0.8 ± 0.8 [A#]	0 ± 0 [A#]	4.71 ± 0 [A#]	1.7 + 1.67 [A#]
Ratio (Ray:Disc)		0.016	0	1.549	0.026
B850					
B. plumosa	Disc	57.6 + 6.27 [a*]	48.8 ± 18.0 [a*]	4.00 ± 1.59 [a*]	43.33 ± 4.41 [ab*]
	Ray	3.2 ± 1.5 [A#]	0 ± 0 [A#]	0.36 ± 0.09 [A#]	0 ± 0 [A#]
Ratio (Ray:Disc)		0.056	0	0.090	0
Middle Canyon					
B. laxa	Disc	23.2 ± 0.8 [*]	58.2 ± 14.7 [*]	7.14 + 2.04 [*]	16.70 ± 6.01 [*]
	Ray	7.2 ± 2.65 [#]	70 ± 20 [##]	27.82 ± 10.97 [##]	18.30 ± 7.26 [#]
Ratio (Ray:Disc)		0.310	1.203	3.896	1.096

laxa. Once again, although higher levels of germination were apparent for *B. laxa* ray seeds when compared to *B. plumosa* ray seeds, and the inverse seemed to be true for disc seeds, these differences were not significant ($P = 0.049$ and 0.057, respectively). The level of germination of disc seeds from the B834 Berm population was significantly greater than was disc germination from the Drainage population. Otherwise, no population differences were found in germination for *B. plumosa*.

All of the plants in the B850 and B834 Drainage populations were lost during the annual spring controlled burns at Site 300. B834 Berm was not burned, but only five *B. plumosa* and three *B. laxa* plants survived to the flowering stage. All eight were disc-derived plants. Because of the limited sample size, we did not perform statistical analyses of the growth and survivorship data.

Laboratory Germination Study

Germination appears to be related to seed age (Fig. 6). A statistical interaction was found among seed age, seed morph, and parent species ($P < 0.0001$). Overall disc germination was greater than overall ray germination, and germination in *B. plumosa* tended to be higher than for *B. laxa*. Linear regression performed for each seed type of each species yielded a significant correlation between seed age and germination for disc seeds in both *B. plumosa* and *B. laxa* (Table 3). The regression for *B. plumosa* disc seeds shows a negative slope: germination decreases slightly as seed age increases. *Blepharizonia laxa* disc seeds show the opposite trend where increasing seed age correlated to a small increase in germination. *Blepharizonia plumosa* ray seeds also show a slight increase in germination with increasing seed age, while germina-

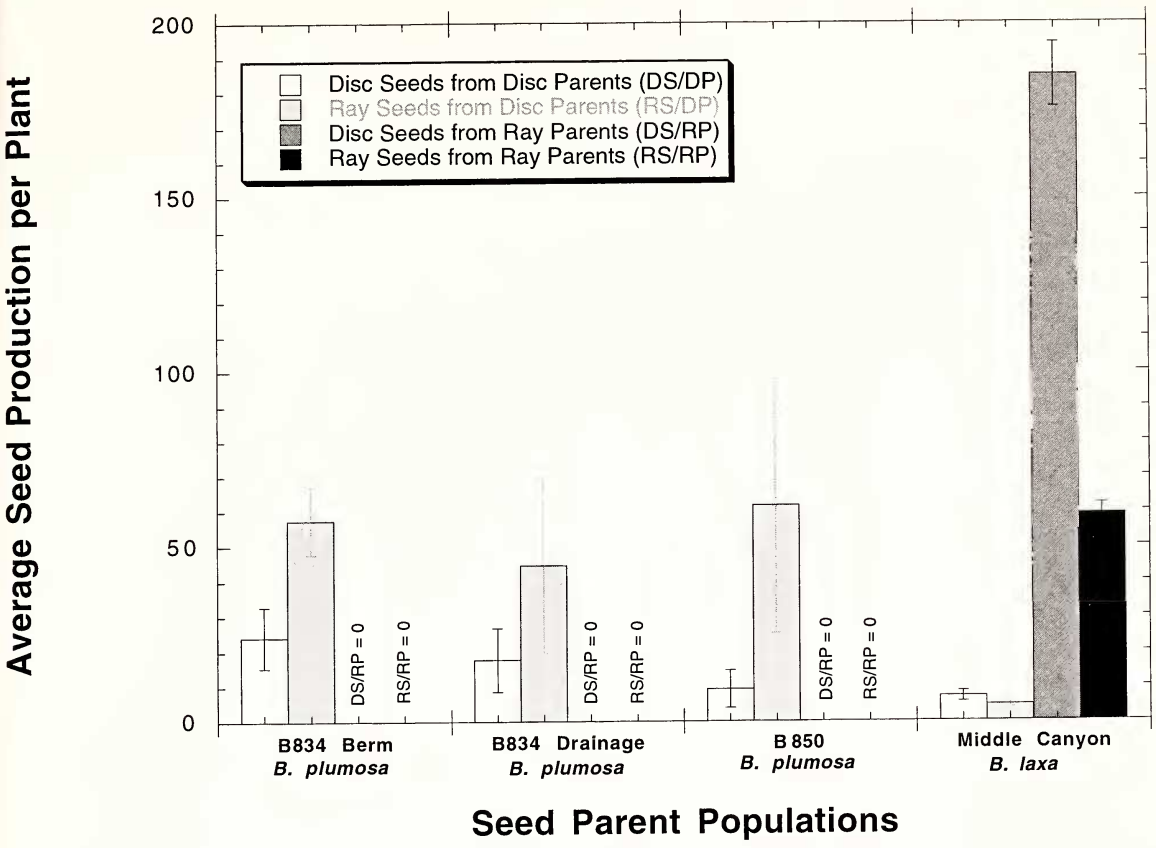

FIG. 5. Average number of mature disc and ray seeds produced from each parent seed type plant (n = 5, error bars = 1 SE).

tion for *B. laxa* ray seeds did not show any significant changes with increasing age.

DISCUSSION

Germination rates and dormancy. The common garden, reciprocal transplant and laboratory germination experiments showed extreme dimorphism in germination percentages of disc and ray seeds within *B. plumosa,* while little dimorphism was found for *B. laxa.* This dimorphism seems to be a common phenomenon within Asteraceae, e.g., in *Heterotheca subaxillaris* var. *subaxillaris* (Baskin and Baskin 1976), *Heterotheca grandiflora* Nutt. (Flint and Palmblad 1978), *Holocarpha macradenia* (DC.) E. Greene (Palmer 1982), *Senecio jacobaea* (McEvoy 1984), *Heterotheca latifolia* (Venable and Levin 1985), *Hemizonia increscens* (Keck) B.D. Tanowitz (Tanowitz et al. 1987), *Heterosperma pinnatum* (Venable et al. 1987), and *Hedypnois rhagadioloides* (Kigel 1992). In all of these studies, disc seeds germinated more rapidly and in higher final proportions than did ray seeds. However, to our knowledge, we are the first to report differences in germination from ray and disc seeds between two closely related species within Asteraceae. These different germination responses are fairly subtle, and the implications are not fully known. Although seed dimorphism is often associated with different germination responses (Esashi and Leopold 1968; Baskin and Baskin 1976; Flint and Palmblad 1978; McEvoy 1984), few have attempted to determine how laboratory results correspond with germination characteristics in the field (Tanowitz et al. 1987).

It has been demonstrated that disc seeds exhibit either no dormancy or significantly shorter dormancy periods in comparison to ray seeds, which exhibit dormancy in all species mentioned above. Several causes of delayed germination for ray seeds have been examined. The most prominent effects on ray seed germination are observed when the pericarp and seed coat are damaged or removed (Palmer 1982; McEvoy 1984; Tanowitz et al. 1987). In these studies, no significant differences were observed in germination rates and final germination proportions between disc seeds and excised ray embryos. McEvoy (1984) suggested that the thick pericarp of the ray seeds acts to physically inhibit germination. However, Palmer (1982) noted that if left intact, the inner nucellar layer (a clear, membranous material) would inhibit germination, potentially acting "in a metabolically active way."

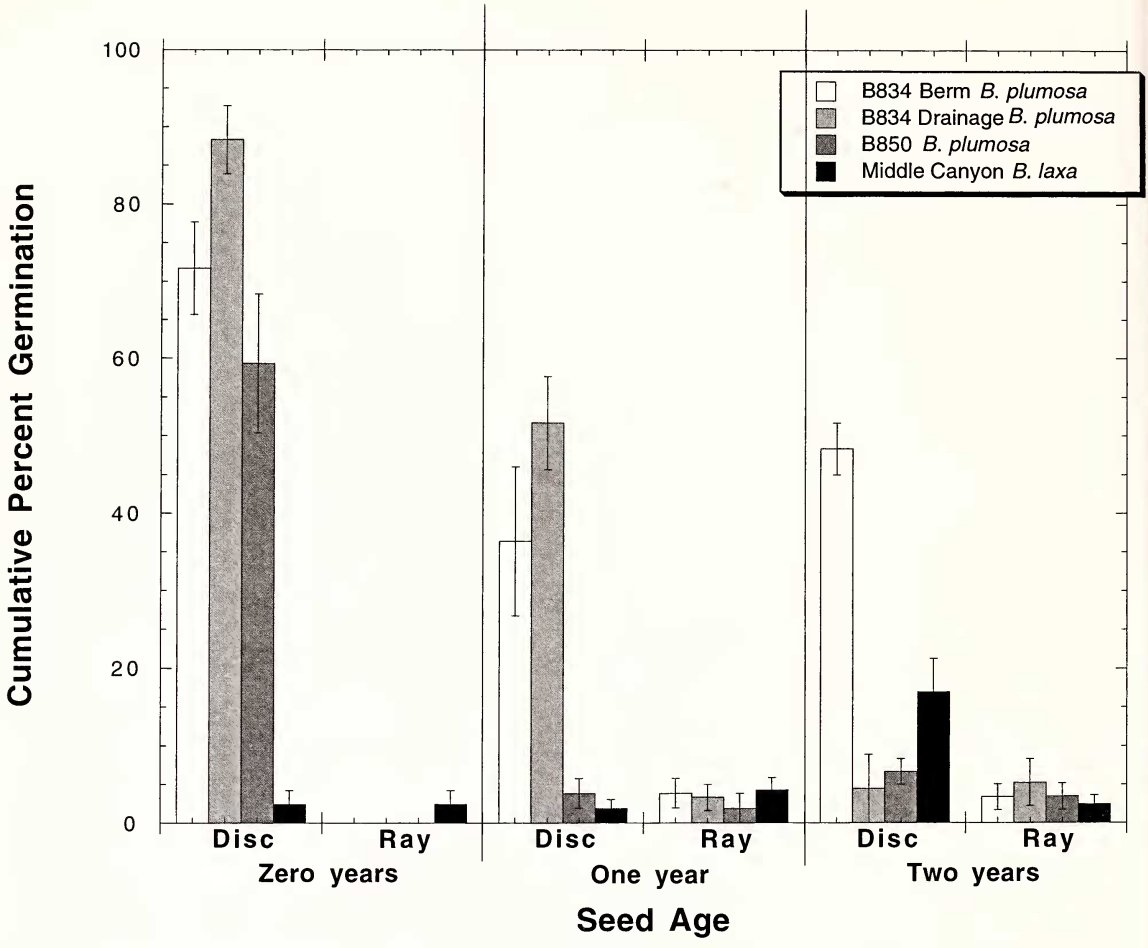

FIG. 6. Germination of disc and ray seeds in the laboratory germination study from three source years (n = 3 for *Blepharizonia plumosa,* n = 6 for *B. laxa,* error bars = 1 SE).

In all cases, the embryos of ray seeds are not dormant, but rather have dormancy imposed on them by maternal tissues (Palmer 1982; McEvoy 1984; Tanowitz et al. 1987).

Multiple environmental factors have been found to influence germination in ray seeds to a greater extent than they influence germination in disc seeds. In several studies, germination of ray seeds was inhibited by darkness, while light availability had little or no effect on disc seed germination (Baskin and Baskin 1976; Flint and Palmblad 1978; Venable and Levin 1985; Venable et al. 1987; Kigel 1992). Venable and Levin (1985) tested this response further and found that germination of ray seeds was negatively correlated with burial depth, and as such they are an important part of the seed bank. In seed bank studies, only ray seeds were found in the soil (Palmer 1982; Venable et al. 1987; Tanowitz et al. 1987). This light response raises questions about the representativeness of the observed germination of ray seeds in our laboratory germination study. Since the germinations were conducted in the dark, except when checked for germination, this could have affected germination

TABLE 3. RESULTS OF GERMINATION BY SEED AGE LINEAR REGRESSION OF LABORATORY GERMINATION EXPERIMENT. ** Regression is significant at $P < 0.017$.

Species	Morph	Regression equation	R^2	n	F	P
B. plumosa	disc	% germination = −0.33 seed age + 0.779**	0.55	25	32.7	<0.0001
B. plumosa	ray	% germination = 0.017 seed age + 0.002**	0.29	25	11.7	0.0021
B. laxa	disc	% germination = 0.077 seed age − 0.099**	0.42	16	13.3	0.0022
B. laxa	ray	% germination = (9.25×10^{-18}) seed age + 0.03	0.06	16	0	1

rates. We may have seen a higher percentage of germination from ray seeds had they been kept in a lighted environment.

Temperature also has an influence on ray seed germination in some species. Baskin and Baskin (1976) found that ray seed after-ripening and subsequent germination in *H. s.* var. *subaxillaris* was inhibited at low temperatures and promoted at high temperatures. They interpreted this response in the context of natural environmental conditions for the winter annual, concluding that ray seeds over-winter for at least one season following dispersal and possibly more, while disc seeds germinate during the first autumn following dispersal. Since our store of seeds used for the laboratory germination study were kept at room temperature, this may also have affected ray seed germination.

Seed production and survivorship. Blepharizonia laxa consistently produced more disc seeds than ray seeds. *Blepharizonia plumosa* derived from disc seeds produced more ray seeds than disc seeds, and ray-seed derived plants produced no seeds at all. As presented in Fig. 5, the majority of the mature seeds produced by *B. plumosa* are ray seeds, which, as discussed above, are less likely to germinate, and if they do germinate, are less likely to produce seeds. Although most of the seeds produced by the *B. laxa* originated from ray-derived plants, this was due to the death of several of the disc-derived *B. laxa* plants just prior to seed maturation. Had this mortality not occurred, the disc-derived *B. laxa* may also have outpaced disc-derived *B. plumosa* plants in seed production since the biomass of the disc-derived *B. laxa* plants was comparable to that of the ray-derived *B. laxa* plants. Also, the disc-derived *B. laxa* plants that died were very large and contained a large number of inflorescences. Although there does not appear to be a survivorship difference between the disc-derived plants of the two species, the survivorship of ray-derived *B. plumosa* plants was lower than that of *B. laxa* ray-derived plants. This difference in survivorship was mirrored by the differences in biomass between the two species.

Interspecific differences and evolutionary consequences. The main differences between the two species appear to be related to the production of dimorphic seeds and the correlation of dimorphism to germination. *Blepharizonia laxa* produces more disc seeds than ray seeds, while this ratio is inverted, and is more extreme, for *B. plumosa.* Germination rates differed between disc and ray seeds in *B. plumosa* but did not differ for *B. laxa. Blepharizonia laxa* disc seed germination increased with age, while *B. plumosa* disc seed germination decreased with age. *Blepharizonia plumosa* ray seed germination increased with age, while *B. laxa* ray seed germination remained the same regardless of age.

The morphology of disc seeds is different between the two species: disc seeds have only a small pappus in *B. laxa,* but have a large pappus in *B. plumosa,* but the ray seed morphology between the two species is more similar (small to nonexistent pappus). The function of seed dimorphism in the ecology of each species may be different. Pappus presence is usually associated with greater dispersal ability and hence differences in pappus presence may be related to differences in seed bank dynamics (Palmer 1982; Venable et al. 1987; Tanowitz et al. 1987) and bet-hedging strategies (Westoby 1981) between the two species.

The evolutionary value of the poor ray seed performance of *B. plumosa* in the field is a puzzle. A question important to many species in Asteraceae is why would a species put so many resources into production of seeds that do not germinate? One explanation could be that ray seeds form the primary seed bank supply, buffering the population for future poor production years. Our study did not fully determine what factors affect ray seed dormancy. As discussed above, light and temperature may play an important role in ray seed germination, and this should be evaluated in future studies.

Areas at Site 300 where *B. plumosa* occurs are subject to routine annual burning. Fire may aid the survival of *B. plumosa* by promoting the growth of native bunch grasses, which may provide a more favorable habitat. However, as we observed, fire also caused direct mortality of seedlings found in the path of a controlled burn. Populations that are routinely burned may therefore depend upon ray seeds, assuming they are a significant part of the seed bank. Reasons for the difference in the prevalence of the two species at Site 300 still elude us. *Blepharizonia laxa* seed exhibits lower germination percentages than *B. plumosa* seed. However, *B. laxa* plants produce more seed for compensation. It is likely that fire plays a differential role in facilitating germination between the two species.

Population differentiation and mitigation. Little differentiation was found between populations of *B. plumosa.* The fact that some differences were seen in the reciprocal transplant experiment germination percentages indicates that some populations may respond better to mitigation than others. Additional experiments with larger sample sizes should be performed prior to any mitigation work. However, we do have a good foundation upon which future experiments relating to population relocation can be performed. The high disc seed germination rates observed for each parent population at each transplant site indicate that seeds from multiple, local populations could be used for this new population. Since the low ray seed germination rate was not mitigated by transplant site/soil type, and not much is known about factors affecting dormancy, ray seeds would not be used as a seed source for this population. At present, it is unknown whether successful long-term establishment of new populations

would be possible. This can only be determined through long-term monitoring and experimental manipulation of both new and existing populations.

Future Studies

Continued monitoring of populations of *B. plumosa* and *B. laxa* within controlled burn areas and comparing them to populations that are not routinely burned will help elucidate the impacts of fire on these populations and the reasons for the different distributions of these two species at Site 300. Factors affecting ray seed dormancy in *B. plumosa* and the role of ray seeds in populations of this species deserve further examination in order to develop the most informed management strategy for this rare plant.

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Literature Cited

Allen, W. H. 1994. Reintroduction of endangered plants. BioScience 44:65–68.

Baldwin, B. G., R. E. Preston, B. L. Wessa, and M. Wetherwax. 2001. A biosystematic and phylogenetic assessment of sympatric taxa in *Blepharizonia* (Compositae–Madiinae). Systematic Botany 26:184–194.

Baskin, J. M. and C. C. Baskin. 1976. Germination dimorphism in *Heterotheca subaxillaris* var. *subaxillaris*. Bulletin of the Torrey Botanical Club 103:201–206.

Bremer, K. 1994. Asteraceae Cladistics and Classification. Timber Press, Inc., Portland, OR.

Byers, D. L. 1998. Effect of cross proximity on progeny fitness in a rare and a common species of *Eupatorium* (Asteraceae). American Journal of Botany 85:644–653.

Carlsen, T. M., J. W. Menke and B. M. Pavlik. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. *Restoration Ecology*. (in press).

Chiariello, N. R. 1989. Phenology of California grasslands. Pp. 47–55 *in* L. F. Huenneke and H. A. Mooney (eds.), Grassland structure and function. Kluwer Academic Publishers, Dordrecht, Netherlands.

CNDDB (California Natural Diversity Database). 1996. File information on *Blepharizonia plumosa* b. *plumosa*. State of California, Department of Fish and Game, Natural Heritage Program, Sacramento, CA.

Dyer, A. R. and K. J. Rice. 1997. Evidence of spatial genetic structure in a California bunchgrass population. Oecologia 112:333–339.

Esashi, Y. and C. A. Leopold. 1968. Physical forces in dormancy and germination of *Xanthium* seeds. Plant Physiology 43:871–876.

Flint, S. D. and I. G. Palmblad. 1978. Germination dimorphism and development in the ruderal weed *Heterotheca grandiflora*. Oecologia 36:33–43.

Gulman, S. L., N. R. Chiariello, H. A. Mooney and C. C. Chu. 1983. Phenology and resource use in three co-occurring grassland annuals. Oecologia 58:33–42.

Hall, L. A. 1986. Transplantation of sensitive plants as mitigation for environmental impacts. Pp. 413–420 *in* T. S. Elias (ed.), Conservation and management of rare and endangered plants. California Native Plant Society, Sacramento, CA.

Harper, J. L. 1977. Population biology of plants. Academic Press, San Diego, CA.

Hickman, J. C. (ed.) 1993. The Jepson manual: higher plants of California, University of California Press, Berkeley, CA.

Hobbs, R. J. and H. A. Mooney. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. Oecologia 67:342–351.

Karis, P. O. and O. Ryding. 1994. Tribe Helenieae. Pp. 521–556 *in* K. Bremer (ed.), Asteraceae Cladistics and Classification. Timber Press, Inc. Portland, OR.

Kigel, J. 1992. Diaspore heteromorphism and germination in populations of the ephemeral *Hedypnois-rhagadioloides* (L) Schmidt, F. W. (Asteraceae) inhabiting a geographic range. Acta Oecologica 13:45–53.

Knapp, E. E. and K. J. Rice. 1994. Starting from seed: genetic issues in using native grasses for restoration. Restoration Ecology Notes 12:40–45.

McEvoy, P. B. 1984. Dormancy and dispersal in dimorphic achenes on tansy ragwort, *Senecio jacobaea* L. (Compositae). Oecologia 61:160–168.

Meagher, T. R., J. Antonovics and R. Primack. 1978. Experimental ecological genetics in *Plantago*. III. Genetic variation and demography in relation to survival of *Plantago cordata*, a rare species. Biological Conservation 14:244–257.

Mooney, H. A., R. J. Hobbs, J. Gorham and K. Williams. 1986. Biomass accumulation and resource utilization in co-occurring grassland annuals. Oecologia 70:555–558.

Morse, S. 1988. Drought tolerance and reproduction in annual plants. Unpublished Ph.D. dissertation. University of California, Berkeley, CA.

Palmer, R. E. 1982. Ecological and evolutionary patterns in *Holocarpha* (Compositae, Madiinae). Unpublished Ph.D. dissertation. University of California, Davis, CA.

Pantone, D. J., B. M. Pavlik and R. B. Kelley. 1995. The reproductive attributes of an endangered plant as compared to a weedy congener. Biological Conservation 71:305–311.

Parsons, L. S. and J. B. Zedler. 1997. Factors affecting reestablishment of an endangered annual plant at a California salt marsh. Ecological Applications 7:253–267.

Pavlik, B. M. 1994. Demographic monitoring and the recovery of endangered plants. Pp. 322–350 *in* M. Bowles and C. Whalen (eds.), Restoration of endangered species. Blackwell Scientific, London.

——— and E. K. Espeland. 1998. Demography of natural and reintroduced populations of *Acanthomintha duttonii*, an endangered serpentinite annual in northern California. Madroño 45:31–39.

PENDLETON, D. F., J. W. MENKE, W. A. WILLIAMS, AND R. G. WOODMANSEE. 1983. Annual grassland ecosystem model. Hilgardia 51:1–44.

PRESTON, R. E. 1996. Status of *Blepharizonia plumosa* (Big Tarplant), its occurrence on LLNL Site 300, and potential project impacts on the species. Report to LLNL Environmental Impact Report (EIR) Update Project File, October 3, 1996.

SAS. 1990. SAS/STAT user's guide, Pp. 891–996. Version 6, 4th ed., vol. 2. SAS Institute Inc., Cary, NC.

SCHOENHERR, A. A. 1992. Natural history of California. University of California Press, Berkeley, CA.

SKINNER, M. AND B. M. PAVLIK. 1994. Inventory of rare and endangered vascular plants of California, 5th ed. California Native Plant Society, Sacramento, CA.

TANOWITZ, B. D., P. F. SALOPEK, AND B. E. MAHALL. 1987. Differential germination of ray and disc achenes in *Hemizonia increscens* (Asteraceae). American Journal of Botany 74:303–312.

VAN DER PIJL, P. 1972. Principles of dispersal in higher plants. Springer-Verlag, Berlin, Germany.

VENABLE, D. L., A. BURQUEZ, G. CORRAL, E. MORALES, AND F. ESPINOSA. 1987. The ecology of seed heteromorphism in *Heterosperma pinnatum* in central Mexico. Ecology 68:65–76.

——— and D. A. Levin. 1985. Ecology of achene dimorphism in *Heterotheca latifolia:* I. Achene structure, germination, and dispersal. Journal of Ecology 73:133–145.

WESTOBY, M. 1981. How diversified seed behavior is selected. American Naturalist 118:882–885.